

## Relationships between dental microwear and diet in Carnivora (Mammalia) – Implications for the reconstruction of the diet of extinct taxa

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### ABSTRACT

Food consumption causes distinct microwear patterns on teeth, especially in mammals that actively masticate food. Here we perform a microwear analysis to assess the relationships between diet and microwear features of diverse Carnivora. Our database includes approximately 230 individuals of 17 extant species having different diets. We analyse both slicing and grinding facets of M1 and m1. The proposed method is reproducible and allows the differentiation, especially on slicing facets, of microwear poles that are significantly distinct from one another. In carnivorans, the microwear features mainly result from their foraging behavior and the proportion of certain food items consumed. We applied our method to extinct taxa such as the amphicyonid *Amphicyon major*. The results on the m1 slicing facet indicate dietary similarities between this large Miocene predator and the extant red fox; results from the m1 grinding facet do not have equivalent in extant taxa, however.

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### 1. Introduction

Carnivora are among the most diverse mammalian orders (McKenna and Bell, 1997; Nowak, 1999; Flynn et al., 2005). Such a great diversity includes a remarkable variety of diets and dental morphologies, from hypercarnivory in meat-eating felids to hypocarnivory such as in the kinkajou (*Potos flavus*), which is a frugivore, or the great panda (*Ailuropoda melanoleuca*), which is an herbivore. A family like the Ursidae documents this dietary diversity well, by including an omnivore (the brown bear *Ursus arctos*), a meat eater (the polar bear *Ursus maritimus*), an insectivore (the sloth bear *Melursus ursinus*), an herbivore (the giant panda *Ailuropoda melanoleuca*), and a foli-frugivore (the spectacled bear *Tremarctos ornatus*) (Sacco and Van Valkenburgh, 2004 and references in Table 1). Past communities of carnivorans (defined thereafter as members of the order Carnivora) also displayed considerable morphological (dentition, locomotor apparatus) and ecological diversity (e.g., Van Valkenburgh, 1988, 1994), which undoubtedly demonstrates that dietary diversity was also great in the past. Many previous studies have used correlations between dental and/or cranio-mandibular features of carnivorans and their dietary specialisation (e.g., Emerson and Radinsky, 1980; Van Valkenburgh and Ruff, 1987; Biknevicius and Ruff, 1992; Biknevicius et al., 1996; Binder and Van Valkenburgh, 2000; Holliday and Stepan, 2004; Therrien, 2005; Anyonge and Baker, 2006; Evans et al., 2007).

However, cranial and dental morphological features partly result from ancestry or systematic affinities (Popowics, 2003; Sacco and Van Valkenburgh, 2004), and therefore, may bias inferences about the diet of some extinct species.

Alternative methods exist. Based on isotope analysis, Feranec (2004) suggested that the sabertoothed cat, *Smilodon fatalis*, from the tar pits of Rancho La Brea, California consumed animals that fed on C<sub>3</sub> vegetation. However, because isotopic ratios depend on the length of the trophic chain, isotopic analysis on extinct mammalian predators are indirect and difficult to interpret (Roth and Hobson, 2000; Bocherens and Drucker, 2003; Sponheimer et al., 2003; Codron et al., 2005). Trace element ratios (Sr/Ca and Ba/Ca) have also been used to infer predator–prey relationships (e.g., Sillen and Lee-Thorp, 1994; Balter et al., 2001), but diagenetic processes often obscure the signal. Analysis of dental micro-abrasion or microwear is an additional method to infer the diet of fossil taxa. Dental microwear analysis consists of a quantification and a comparison of different types of microwear resulting from the abrasion of dental surface caused by consumption and mastication of food during the last days of life of an animal (Rensberger, 1978; Teaford and Oyen, 1989). Until now, such analyses were generally applied to extant primates and ungulates to reconstruct the diet, then the environment of their fossil relatives (Walker et al., 1978; Janis, 1990; Teaford, 1991; Solounias and Sempereon, 2002; Merceron et al., 2004, 2005a,b,c; Merceron and Ungar, 2005; Merceron et al., 2006; Merceron and Madelaine, 2006). Microwear analyses were also applied to extant and/or extinct carnivorans in a couple of studies, with promising, though heterogeneous, results. Taylor and Hannam (1986) used 32 specimens belonging to 12 different species

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**Table 1**  
Diets and references of recent taxa studied here (sorted by diet)

Diet	Vernacular name	Species	References
Meat eater	Malagasy civet	<i>Fossa fossana</i>	Nowak (1999), Muñoz Garcia and Williams (2005)
	Polar bear	<i>Ursus maritimus</i>	De Master and Stirling (1981), Nowak (1999)
	Serval	<i>Leptailurus serval</i>	Estes (1991), Nowak (1999), Muñoz Garcia and Williams (2005)
Bone eater	Spotted hyena	<i>Crocuta crocuta</i>	Estes (1991), Nowak (1999)
	Stripped hyena	<i>Hyaena hyaena</i>	Rieger (1981), Estes (1991), Nowak (1999), Muñoz Garcia and Williams (2005)
Piscivore	European river otter	<i>Lutra lutra</i>	Herfst (1984), Hainard (1989), Nowak (1999), Muñoz Garcia and Williams (2005), Tüzün and Albayrak (2005)
Herbivore	Great panda	<i>Ailuropoda melanoleuca</i>	Chorn and Hoffman (1978), Schaller et al. (1989), Nowak (1999)
	Lesser panda	<i>Ailurus fulgens</i>	Roberts and Gittleman (1984), Nowak (1999), Muñoz Garcia and Williams (2005)
Larva and worm eater	Falanouc	<i>Eupleres goudotii</i>	Garbutt (1999), Nowak (1999)
Insectivore	Sloth bear	<i>Melursus ursinus</i>	Nowak (1999), Muñoz Garcia and Williams (2005)
	Stripped mongoose	<i>Mungos mungo</i>	Estes (1991), Nowak (1999)
	Slender mongoose	<i>Galerella sanguinea</i>	Estes (1991), Nowak (1999), Muñoz Garcia and Williams (2005)
	Spectacled bear	<i>Tremarctos ornatus</i>	Nowak (1999)
Frugivore	Kinkajou	<i>Potos flavus</i>	Ford and Hoffman (1988), Nowak (1999), Muñoz Garcia and Williams (2005)
Malacophage	Sea otter	<i>Enhydra lutris</i>	Estes (1980), Hainard (1989), Nowak (1999)
Omnivore	European badger	<i>Meles meles</i>	Hainard (1989), Nowak (1999), Boesi and Biancardi (2002), Lanszki (2004), Virgós et al. (2004), Muñoz Garcia and Williams (2005)
	Red fox	<i>Vulpes vulpes</i>	Hainard (1989), Nowak (1999), Muñoz Garcia and Williams (2005)

of Viverridae. They showed the presence of two types of wear, pits and furrows. Their observations on the whole tooth row, without reference to facets and based on a low number of specimens, are difficult to interpret. Van Valkenburgh et al. (1990) analysed the microwear of 90 specimens of large carnivores belonging to nine extant species. They showed possible relationships between microwear patterns on the labial facet of the lower carnassial paraconid and bone consumption. Moreover, they demonstrate that the sabertoothed cat *S. fatalis* avoided bones during killing and feeding. Anyonge (1996) confirmed the results of Van Valkenburgh et al. (1990), based on an analysis of the canine teeth in six extant species and *S. fatalis*. In his study of early Paleocene mammals of Colorado, Dewar (2003a) dealt more with the surface and the wear level of dental facets than with the relationships between diet and microwear. In his subsequent analysis on microwear types in carnivores (Dewar, 2003b), this author used the paracone of the first upper molar (M1) and included only six extant species, which provides limited useful information to infer the diet of fossil taxa.

It is not currently possible to compare the results of these previous studies because they used different dental facets generally from small samples (in terms of extant species and/or number of individuals) that did not document a wide variety of diets. In addition, some fundamental questions remained unsolved. Is microwear analysis applicable to any species of Carnivora? Can we use the same facets in any species of the order to make informative comparisons? Can the methodological approach applied to primates and ungulates also be applied to carnivores, and if so, can microwear analysis be applied to

fossil taxa and help to reconstruct their diet? The goal of the present study is to provide some answers to these questions and to assess the origin of microwear in carnivores. We propose a precise methodological approach to test whether the microwear analysis can be applied to any carnivores. The relationship between diet and dental microwear pattern is based here on an original database that is the most complete one ever published for carnivores. Because this study aims to reconstruct the diet of extinct taxa, we also propose a reconstruction of the diet of two species of Amphicyonidae, an extinct family of generalist carnivores, from the middle Miocene of France.

## 2. Material

### 2.1. Recent material

Extant species have been chosen with regard to their alimentary preferences. Each representative diet of Carnivora is illustrated by at least one extant species. The diet assigned to each extant species accounts for at least 70% of ingested food (Table 1). Our database contains 228 specimens belonging to 17 species (referred to the nine families of terrestrial carnivores; Table 2). Only wild-caught and adult specimens are included to avoid biases resulting from artificial diet and lactation. See Table 2 for the condensed database and Appendix A for the complete one. This sample is chosen to be as representative as possible (without intrinsic bias) of the large range of diets, and therefore potential microwear patterns, within carnivores.

### 2.2. Fossil material

There is little doubt that extinct hypercarnivorous taxa such as felids were meat eaters. In contrast, reconstructing the diet of an extinct taxon

**Table 2**  
Observed sample (sorted by name)

Species	Vernacular name	Family	Number of specimens	Specimens analysed on the slicing facet	Specimens analysed on the grinding facet
<i>Ailuropoda melanoleuca</i>	Great panda	Ursidae	4	4	3
<i>Ailurus fulgens</i>	Lesser panda	Ailuridae	5	3	4
<i>Crocuta crocuta</i>	Spotted hyena	Hyaenidae	15	13	5
<i>Enhydra lutris</i>	Sea otter	Mustelidae	4	4	4
<i>Eupleres goudotii</i>	Falanouc	Eupleridae	9	7	0
<i>Fossa fossana</i>	Malagasy civet	Eupleridae	14	14	12
<i>Galerella sanguinea</i>	Slender mongoose	Herpestidae	21	17	11
<i>Hyaena hyaena</i>	Stripped hyena	Hyaenidae	6	5	3
<i>Leptailurus serval</i>	Serval	Felidae	12	11	9
<i>Lutra lutra</i>	European river otter	Mustelidae	20	20	18
<i>Meles meles</i>	European badger	Mustelidae	23	17	20
<i>Melursus ursinus</i>	Sloth bear	Ursidae	4	4	2
<i>Mungos mungo</i>	Stripped mongoose	Herpestidae	13	9	8
<i>Potos flavus</i>	Kinkajou	Procyonidae	21	14	10
<i>Tremarctos ornatus</i>	Spectacled bear	Ursidae	2	2	2
<i>Ursus maritimus</i>	Polar bear	Ursidae	19	16	18
<i>Vulpes vulpes</i>	Red fox	Canidae	25	25	25

**Table 3**  
Extinct taxa

Determination	No. specimen	Analysed teeth
<i>Amphicyon major</i>	MNHN Sa 1*	P4
	MNHN Sa 2	P4d, M1d
	MNHN Sa 3	M1g
	MNHN Sa 37	m1g
	MNHN Sa 4	M1d
	MNHN Sa 5	M1g
	MNHN Sa 36	m1d
	MNHN Sa 35	m1g
	MNHN Sa 45	m1d
	MNHN Sa 844	M1d, m1d
<i>Pseudocyon sansaniensis</i>	MNHN Sa 207*	m1d

Encircled numbers may correspond to the same individual.\*: Holotype.

that was a generalist as inferred from dentition is more challenging because, by definition, it probably includes various items (fruits, leaves, meat, bones) the proportions of which remain to be determined. We have chosen the Amphicyonidae. This family includes medium- to large-sized taxa generally mesocarnivores, although there are more specialised taxa, some with a reduced dentition (e.g., *Thaumastocyon*, *Haplocyonoides*) compared to the average amphicyonid, and some emphasizing hypocarnivory (e.g. *Pseudarctos*, *Ictiocyon*). If the portion of each kind of item cannot be determined by morphology only, microwear analysis may help to identify an extant equivalent species. The amphicyonid material studied is composed of individuals from the middle Miocene of Sansan, southwestern France (aged ca.14.8 Ma). Since its discovery (Lartet, 1836), this locality has yielded an extremely rich fauna that includes 78 mammalian species, of which 20 are carnivores (Ginsburg and Bulot, 2000). The best known species of Carnivora is *Amphicyon major*, with a minimum number of 7 individuals. This species displays a strong sexual dimorphism (Ginsburg, 1961), with a body weight ranging from approximately 120 kg for females to more than 200 kg for males (Viranta, 1996), but extreme estimates have also been proposed (630 kg; Legendre and Roth, 1988). *A. major* is known from the middle Miocene, mainly in western Europe (Ginsburg, 1999). A second species, *Pseudocyon sansaniensis*, is also included here for comparison (Table 3). This is a smaller-sized species, approximately the body weight of a female of *A. major* (Viranta, 1996). It is much scarcer than the latter species and known only from the middle Miocene of France and Germany (Ginsburg, 1999). This material is stored in the collections of the Muséum national d'Histoire naturelle (MNHN), Paris. Previous authors inferred the diet of *Amphicyon* and *Pseudocyon* species from dental, cranial, and/or postcranial morphology. From the dental morphology, dental wear pattern, and cranial morphology, Viranta (1996) interprets *A. major*, *A. giganteus*, *A. pannonicus*, *A. gutmanni* as “bone-crushing mesocarnivores” (i.e., meat eaters able to switch to herbivorous diet; Viranta, 1996, p. 44); from the molar morphology she also proposed that *Pseudocyon* species had a carnivorous (i.e., primarily meat) diet and more reduced adaptations to bone crushing than in *Amphicyon*. Based on dental and postcranial morphology, the North American species of *Amphicyon* are interpreted as large-sized terrestrial omnivores (Hunt, 2003). Using the ratio between the total grinding area of lower molars and the total blade length of m1, Sorkin (2006) interprets the diet of the North American *Amphicyon longiramus* as “primarily carnivorous”, i.e., including less than 10% of plant material. This result is not surprising since the species used by Sorkin, *A. longiramus* from the early Hemingfordian (early Miocene) of Florida, USA, is not specialised as are later *Amphicyon* such as *A. major* or *A. frendens*, which display, for example, enlarged crushing molars. It is worth noting that *A. longiramus* is not assigned to *Amphicyon* in a recent review of the North American material (Hunt, 2003). Ginsburg (1999, p. 118) states that *Amphicyon* did cut the flesh as the felids and crushed the bones as the hyaenids. The duality of the dentition of amphicyonines (with both shearing and crushing functions on carnassials and molars) was also implicitly described by other authors (e.g., Hunt, 1998). In

species of *Amphicyon* also, the shearing function of the carnassial is preserved, although these species display a remarkable development of the crushing function with the enlargement of M1–3/m2–3.

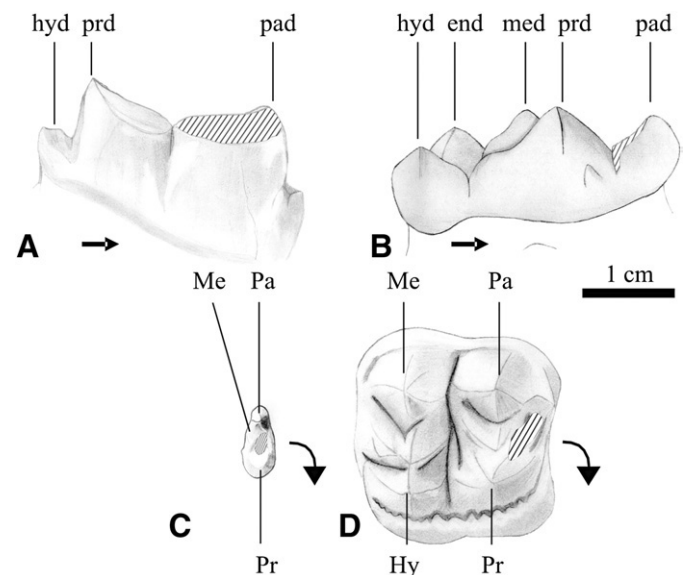
### 3. Method

Scanning electron microscopy (SEM) is generally preferred to optical stereomicroscopy to study microwear, although the latter is cheaper and less invasive. Solounias and Semprebon (2002) proposed a method using optical stereomicroscopy. Despite moderate reproducibility Semprebon et al. (2004) concluded that diet can be inferred with this technique. Merceron et al. (2004, 2005a) modified this procedure by adding a snapshot before the quantification of microwear, which would limit the intra- and inter-observer errors. This method is reliable, cheaper than a SEM and non-invasive but needs a great database and its application to fossils depends on fossilization and taphonomic conditions.

#### 3.1. Teeth and dental facets

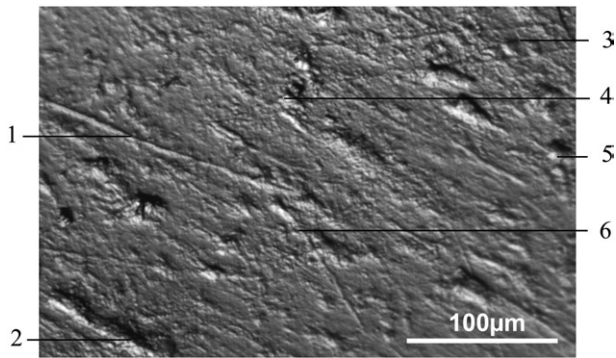
Due to fundamental differences in their ancestry and their biology, the choice of the studied teeth and facets cannot be the same in, e.g., ungulates and carnivores. Thus, unlike ungulates, there is no simultaneous occlusion of cheek teeth in carnivores (Janis, 1995). Moreover, carnivores cannot move mandibles laterally (Hiiemae, 1978; Gorniak and Gans, 1980). Carnivore dental morphology is also modified; slicing and grinding areas are clearly differentiated along the tooth row. The carnassials (P4 and m1) are mainly responsible for the slicing function (Butler, 1946; De Muizon and Lange-Badré, 1997), while the back of the tooth row is devoted to the grinding function (from M1 and m1 talonid backwards). Hyaenids are a peculiar case in that their crushing function is located mostly on the third premolars (Biknevicius, 1996; Rensberger, 1997).

Microwear analysis is applied in priority to the lower carnassials. These teeth are diagnostic of the order Carnivora. They present two different functions (slicing and grinding) and are very steady in morphology and size among species (Meiri et al., 2005). This choice also enables comparisons between all species. In ungulates, m2 is



**Fig. 1.** Position of the studied facets on the right molars of two species: A. *Crocuta crocuta* m1 vestibular view, B. *Ailuropoda melanoleuca* m1 vestibular view, C. *Crocuta crocuta* M1 occlusal view, D. *Ailuropoda melanoleuca* M1 occlusal view. end: entoconid, Hy: hypocone, hyd: hypoconid, Me: metacone, med: metaconid, Pa: paracone, pad: paraconid, Pr: protocone, prd: protoconid. Hatched areas correspond to studied facet, arrows to the tooth row orientation. Scale bar: 1 cm.





**Fig. 2.** Detail of an *Amphicyon major* slicing facet illustrating the various types of dental microwear in Carnivora. 1: fine scratch; 2: broad scratch; 3: broad pit; 4: gap; 5: ovoid pit; 6: small pit. Scale bar: 100  $\mu$ m.

generally preferred because of its median level of wear compared to other molars (Gordon, 1982). In carnivorans, however, this tooth is either absent or strongly reduced in some families of Carnivora (Felidae, Hyaenidae and Mustelidae). M1 is used for the moulding of the grinding facet when the latter is not easily approachable (limited access) on m1, as in *Eupleres goudotii*, *Galerella sanguinea*, and *Mungos mungo*.

The choice of the facets must allow reproducibility. Two complementary types of wear are therefore analysed; one due to the slicing phase, the other due to the grinding phase of chewing. The two facets chosen for this study are representative of different chewing phases, are easily accessible, and are present in all Carnivora species. Therefore, the slicing phase is analysed on the labial facet of m1 paraconid (Fig. 1A and B) and the chewing phase on the meso-labial facet of M1 protocone (Fig. 1C and D) (corresponding to the “facet nine” in primates after Grine (1987), Merceron et al. (2005a) and Merceron et al. (2006)).

In fossil taxa and/or in poorly preserved specimens that do not document these facets, we use their analogous facets (i.e. those in contact when upper and lower tooth rows occlude). They are, for the

grinding phase, the lingual facet of m1 hypoconid and, for the slicing phase, the distolingual facet of P4 metacone. According to Teaford and Walker (1984), analogous facets have a highly similar wear in the primates and are qualified homologous. We test this homology using slicing and grinding facets of the upper and lower right tooth rows of *Meles meles*.

### 3.2. Moulding

The procedure of Merceron et al. (2004, 2005a) is applied here, using the same instruments.

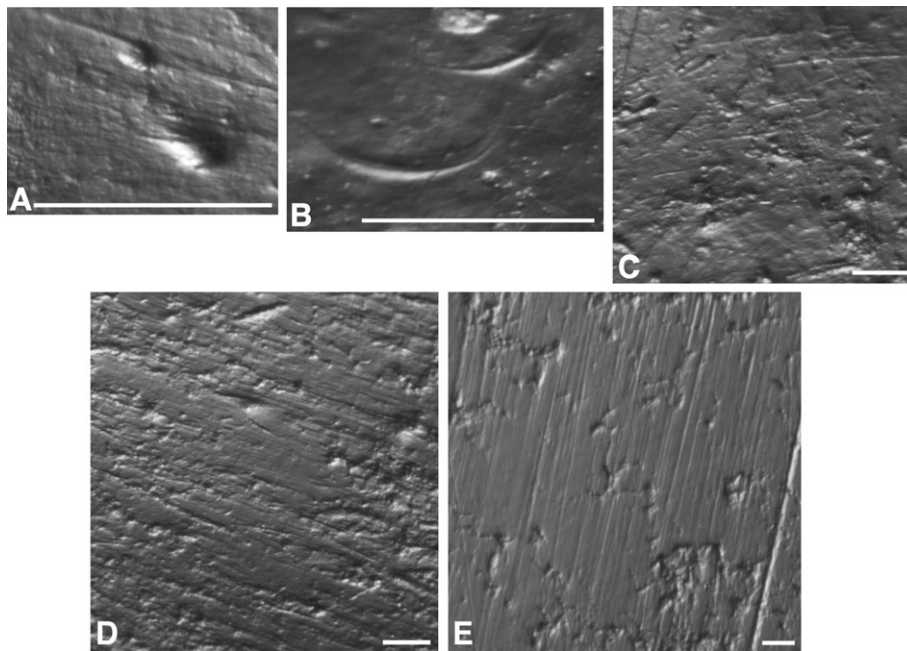
### 3.3. Image processing and acquisition of data

The resin mouldings are observed by transmitted light with an optical stereomicroscope (MZ 16 Leica®) (CLS 150X Leica®). Snapshots are made with a camera (DFC 320 Leica®) and the software IM 500 (Leica®) to the magnification  $\times 63$ . A 300  $\mu$ m-side square (0.09 mm<sup>2</sup>) is selected and then analysed on the photograph of each facet with the software Optimas version 6.51 (Media Cybernetics®). The dimensions of the square permit the analysis of the facets of the smallest taxa among carnivorans.

The variables measured (Fig. 2) are the numbers of scratches (N S); wear whose width/length ratio is less than 1/4 (Solounias and Hayek 1993; Merceron et al., 2004, 2005a,b,c); pits (N P): ratio greater than 1/4; broad scratches (N bS): width greater than 5  $\mu$ m; broad pits (N bP): diameter greater than 5  $\mu$ m; ovoid pits (N ovP): broad oval pits with definite margin (Fig. 3A); and gaps (N G): broad pits with poorly defined margin. Numbers of fine scratches (N fS) and fine pits (N fP) are inferred from other variables as N P is the sum of N bP and N fP and N S, the sum of N bS and N fS (Fig. 2). Special features, such as curved scratches (N cS) are noted too (Fig. 3B).

### 3.4. Statistical data processing

We use the software Statistica version 7.1 (Statsoft®) for statistical tests. The normality of the distribution of observations and the



**Fig. 3.** Examples of features and facets. A. Ovoid pits on the grinding facet of MNHN CG 1854-189 (*Potos flavus*) ( $\times 189$ ); B. Curved scratches on the grinding facet of MNHN CG 1929-1531 (*Hyaena hyaena*) ( $\times 63$ ); C. Grinding facet of MNHN CG 1928-297 (*Ursus maritimus*) ( $\times 63$ ); D. Slicing facet of MNHN CG 1995-1207 (*Lutra lutra*) ( $\times 63$ ); E. Numerous scratches on the slicing facet of MNHN CG 2000-481 (*Ailuropoda melanoleuca*) ( $\times 63$ ). Scale bar: 100  $\mu$ m.

**Table 4**

Comparison of the lower and higher homologous facets of *Meles meles*: synthesis of the nonparametric ANOVA of Kruskal–Wallis for the grinding facet and variance analysis for the slicing one

Facet	N S	N P	N bS	N bP	N fS	N fP	N cS	N ovP	N G
Grinding	0.001	0.023	0.414	0	0	0.254	0.558	0.367	0
Slicing	0.079	0.317	0.508	0.4	0.095	0.191	0.453	0.435	0.241

$p < 0.05$  in both cases.

homeoscedasticity are checked on the sets “diets” and “species” thanks to the tests of Shapiro–Wilk and Levène, respectively. The latter indicates significant differences between variances, which prevents the application of parametric ANOVA to the data file. After a log-transformation of data, homeoscedasticity still not being apparent, the unrefined variables are submitted to a nonparametric Kruskal–Wallis ANOVA. It is supplemented by pair-to-pair Mann–Whitney tests.

It is important to note that analogies between the lower slicing facet and the upper one whose values are normally distributed with appropriate homeoscedasticity, are evaluated by a parametric ANOVA.

Results are presented both in principal components analysis and in bivariate plots. Principal components analysis is realised on: N fS, N bS, N fP, N bP, N G for both grinding and slicing facets. The active sample for statistical analysis is exclusively composed of living taxa to distinguish more precisely the differences in the microwear produced by known diets. Extinct taxa are then added to statistical plots without influencing their calculation.

## 4. Results

### 4.1. Validation of the method

According to the nonparametric Kruskal–Wallis ANOVA, the number of scratches (N S), pits (N P), broad pits (N bP), fine scratches (N fS), and gaps (N G) on the homologous grinding facets of *Meles meles* differ significantly at  $p < 0.05$  (Table 4). A comparison of their variance does not show any analogy between the facets. Thus, we chose to analyse the grinding phase of the sample on the upper facet (mesiolabial facet of M1 paracone) only, because it is more easily observable than the lower facet.

The statistical test (parametric ANOVA) shows that the tested variables are not significantly different for the analogous slicing facets at the  $p < 0.05$  (Table 4). These facets will thus be treated identically hereafter.

The significance of the 0.09 mm<sup>2</sup> square of reference on facets is tested by analysing ten squares of 300 µm side differently positioned on the same facet. This test has been applied to the grinding facet of *Ursus maritimus* (MNHN CG 1928–297) and to the slicing facet of *Enhydra lutris* (MNHN CG 1962–2678). In both cases, standard deviations and typical means error are lower than those of the whole dataset for the facet concerned. The validity of the counting square is thus

**Table 5**

Eigen values and associated statistics for the variables N fS, N fP, N bS, N bP and N G on the two facets

Facet	Axis	Eigen value	% Complete variance	Eigen value cumul	% cumul
Grinding	1	1.48	29.60	1.48	29.60
	2	1.17	23.47	2.65	53.07
	3	1.03	20.53	3.68	73.61
	4	0.82	16.48	4.50	90.08
	5	0.50	9.92	5.00	100.00
Slicing	1	2.02	40.41	2.02	40.41
	2	1.09	21.84	3.11	62.25
	3	0.90	17.96	4.01	80.21
	4	0.66	13.27	4.67	93.48
	5	0.33	6.52	5.00	100.00

**Table 6**

Variables contribution based on the correlation matrix

Facet	Variable	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Grinding	N bS	0.00	<b>0.56</b>	0.00	0.38	0.06
	N bP	<b>0.33</b>	0.03	0.29	0.01	<b>0.34</b>
	N fS	<b>0.36</b>	0.16	0.01	0.09	<b>0.37</b>
	N fP	0.13	0.01	<b>0.66</b>	0.06	0.15
	N G	0.17	0.24	0.04	<b>0.47</b>	0.08
Slicing	N bS	0.08	0.27	<b>0.53</b>	0.10	0.02
	N bP	<b>0.32</b>	0.03	0.20	0.01	0.45
	N fS	0.14	0.23	0.21	<b>0.42</b>	0.00
	N fP	<b>0.35</b>	0.07	0.05	0.01	<b>0.53</b>
	N G	0.12	<b>0.40</b>	0.00	<b>0.47</b>	0.00

Bold datas refer to the most contributive variable(s) on each axis for both facets.

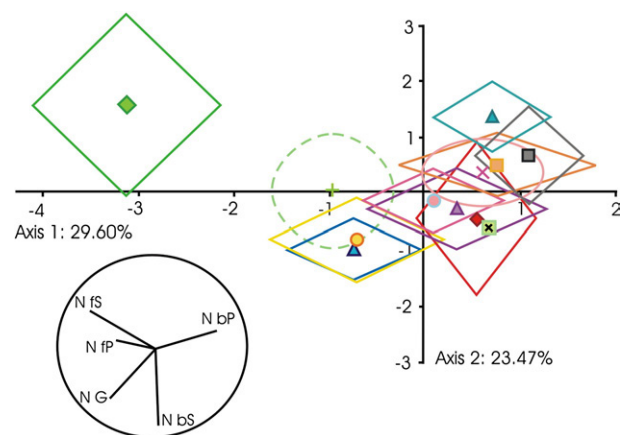
established regardless of its position on the facet. This allows the use of small-sized species having tiny dental facets (approximately 0.1 mm<sup>2</sup>).

To test intra-observer reproducibility, ten countings are carried out in the same square (in several sessions), on the slicing facet of MNHN CG 1880–2542 (*Eupleres goudotii*) and on the grinding facet of MNHN CG 1928–297 (*Ursus maritimus*). Here, the standard deviations and typical errors on mean are lower than those of the square itself. Reproducibility intra-observer is thus established. However, a test including additional specimens would be necessary as well as a check of reproducibility inter-observer.

### 4.2. Principal components analysis (PCA)

N P and N S being dependent from N bP, N fP, N bS and N fS, they are not included in this analysis.

On the grinding facet, the combination of the first two axes accounts for only 53.07% of the information (Table 5) and the results exposed must be considered as doubtful. The first axis is governed by the N bP and N fS (Table 6) in opposite ways. The second one is mainly representative of the number of broad scratches. We can determine from the position of the individuals on these axes that herbivores (*Ailurus fulgens* and *Ailuropoda melanoleuca*) are distinguished by a proportion of fine scratches much greater than in any other taxa (Fig. 4). Piscivores and malacophages are indistinct on this graph but there is another microwear pole, determined by the number of broad pits, formed by insectivores, meat eaters, bone eaters and frugivores. Not surprisingly, omnivores cover a great range of patterns, the European badger being closer to piscivores, herbivores and malacophages and the



**Fig. 4.** Principal components analysis on the grinding facet including all specimens, axes 1 (29.60%) and 2 (23.47%). N bS: number of broad scratches; N fS: number of fine scratches; N bP: number of broad pits; N fP: number of fine pits; N G: number of gaps. Diets represented by their mean (dot) and standard deviation (diamond or circle). *Leptailurus serval*, *bone eater*, *piscivore*, *frugivore*, *herbivore*, *insectivore*, *malacophage*, *meat eater*, *Vulpes vulpes*, *Meles meles*, *Amphicyon major*, *Pseudocyon sansaniensis*.

red fox to the meat-eaters, insectivores and frugivores. This distribution of diets and species reflects the results obtained with the Kruskal–Wallis and Mann–Whitney tests. However, the grinding facet is less representative than the slicing one according to these tests (a less significant number of variables allowing the differentiation of the diets). Herbivores, the most clearly discernible group on the grinding facet, are characterized by a great number of scratches (average: 54.50). Other diets (insectivore, frugivore, piscivore, meat eater, and bone eater) differentiate more on the slicing facet. The following axes give similar information. Axis three, supporting mainly the information of the number of fine pits (Table 6), permits to differentiate bone eaters from all other diets. As the results on this facet are not totally convincing, they are not developed in the bivariate plots.

Fig. 5 illustrates the distribution of individuals on the three first axes for the slicing facet. On this facet, the first axis expresses 40.41% of the original variance (Table 5), and is mainly informative for N bP and N fP (Table 6), while the second axis expresses 21.84% of the original variance and N G is the main variable that contributes to this component. Combining the first three axes, 80.21% of the original variance is expressed and N bP, N fP, N G and N bS contribute to the information given on these axes. This representation reveals a clear differentiation of herbivores, according to their number of fine scratches, whereas the piscivores and *Leptailurus serval* are characterized by their high number of pits. These three diets discriminate well on the first axis (Fig. 5A). Malacophages and the eaters of larvae and worms can also be grouped together and isolated from the other diets on this axis. They are separated on the third axis (Fig. 5B). Insectivores, bone eaters, meat eaters and frugivores discriminate better on axes

**Table 7**

Results of the Kruskal–Wallis ANOVA on the two facets applied to ten species representative of a diet and to the diets,  $p < 0.05$

Facet	Sorting by	N S	N P	N bS	N bP	N fS	N fP	N ovP	N G	N cS
Grinding	Species	0	0.013	0	0	0	0.006	0	0	0.252
	Diets	0	0	0	0	0	0.005	0	0	0.08
Slicing	Species	0	0	0	0	0	0	0.007	0	
	Diets	0	0	0	0	0	0	0.007	0	

two, three and four. For example, frugivores are totally isolated from meat and bone eaters on multivariate plots representing axes one and three. On the slicing facet the red fox enters within the range of insectivores, frugivores, meat eater and bone eater and the European badger is divided in two subgroups. One is located between herbivores and larvae and worm eaters, while the other one has the same variation as *Vulpes vulpes*.

#### 4.3. Statistical tests

Results are summarized in Appendix A.

##### 4.3.1. Grinding facet (Fig. 3C)

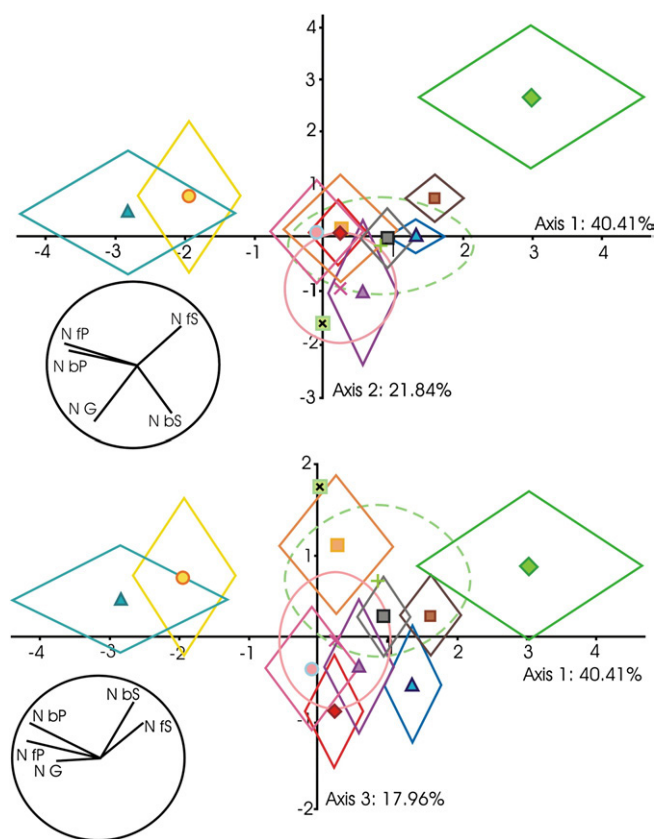
The software Statistica enables analysis of a maximum of ten “groups” simultaneously by a Kruskal–Wallis ANOVA. Ten species representative of a diet and including the greatest number of exploitable specimens are selected for this analysis: the red panda, *Ailurus fulgens*, herbivore; the spotted hyena, *Crocuta crocuta*, bone eater; the sea otter, *Enhydra lutris*, malacophage (because the diet of the sea otter may include crustaceans we prefer this name to “molluscivore” used in previous studies; e.g., Van Valkenburgh, 1989); the falanouc, *Fossa fossana*, meat eater (i.e., flesh from vertebrates); the slender mongoose, *Galerella sanguinea*, insectivore; the river otter, *Lutra lutra*, piscivore; the serval, *Leptailurus serval*, meat eater; the kinkajou, *Potos flavus*, frugivore; the polar bear, *Ursus maritimus*, meat eater and the red fox, *Vulpes vulpes*, omnivore. All variables show statistically significant differences to distinguish these species (Table 7). The same tests are applied to the diets. Results of the Kruskal–Wallis ANOVA (Table 7) confirm initial observations: the species and diets statistically give the same result. Differences between these species for these parameters then correspond to differences between diets. A summary of the results obtained on this facet thanks to the Mann–Whitney test is presented in Appendix A. The variables making a clear distinction in diets are the number of scratches: N S, the number of broad pits: N bP, and the number of gaps: N G.

##### 4.3.2. Slicing facet (example Fig. 3D and E)

The ten species chosen for the Kruskal–Wallis test on the slicing facet are identical to those used for the grinding facet except that the falanouc, *Eupleres goudotii* (eater of larvae and worms) replaces *Fossa fossana* (results in Table 7).

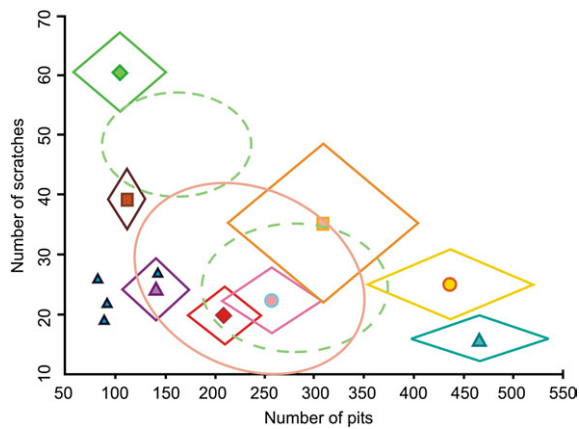
Table 7 also summarizes the results of the nonparametric ANOVA applied to the diets on the slicing facet (see Appendix A for results of the Mann–Whitney test on this facet) without taking into account N cS. Species and diets statistically give the same result and particularly on the most informative variables, which distinguish the various diets (N S, N P, N fS, N fP). Differentiating diets on the slicing facet is clearer than on the grinding one. As good identifying factors, N P and N S are used to construct bivariate plots on the slicing facet (Fig. 6). See Appendix A for a summary of the results used for the graphs.

Some diets are distinguished by a small number of scratches (bone eaters, malacophages, herbivores, frugivores) and others by a small number of pits (meat eaters, insectivores, piscivores, *Leptailurus serval*) (Fig. 6). No species have both a great number of pits and scratches whereas the opposite is true for the bone eaters and malacophages. Nevertheless, some gaps in these graphics are filled by omnivores who show a greater variability in microwear patterns than



**Fig. 5.** Principal components analysis on the slicing facet including all specimens. A. Axes 1 (40.41%) and 2 (21.84%); B. axes 1 (40.41%) and 3 (17.96%). N bS: number of broad scratches; N fS: number of fine scratches; N bP: number of broad pits; N fP: number of fine pits; N G: number of gaps. Diets represented by their mean (dot) and standard deviation (diamond or circle). ♦ *Leptailurus serval*, ♦ bone eater, ♦ piscivore, ♦ frugivore, ♦ herbivore, ♦ insectivore, ♦ malacophage, ♦ meat eater, ♦ larvae and worm eater, ♦ *Vulpes vulpes*, ♦ *Meles meles*, ♦ *Amphicyon major*, ♦ *Pseudocyon sansaniensis*.





**Fig. 6.** Number of scratches as a function of the number of pits on the slicing facet of extant specimens. Diets represented by their mean (dot) and standard deviation (diamond) except “Malacophage” represented by four specimens and *Vulpes vulpes* and *Meles meles* represented by their total variation.  $\diamond$  *Leptailurus serval*,  $\diamond$  bone eater,  $\diamond$  piscivore,  $\diamond$  frugivore,  $\diamond$  herbivore,  $\diamond$  insectivore,  $\triangle$  malacophage,  $\diamond$  meat eater,  $\diamond$  larvae and worm eater,  $\circ$  *Vulpes vulpes*,  $\diamond$  *Meles meles*.

specialised consumers (two-dimensional distribution of all individuals on the slicing facet in Appendix A).

Some species are clearly distinct from others. Herbivores are distinguished by a lower number of pits (104.2 on average) and a more important number of scratches (60.4 on average) (Fig. 3E) than other species. The larvae and worm eaters are the only ones having a medium number of scratches (40 scratches per facet on average) and a low number of pits. Piscivores and *L. serval* have a high number of pits, the latter having in addition a very low number of scratches. *L. serval* shows a remarkable type of wear on the slicing facet (Fig. 6). Its food includes rodents and other small vertebrates (Estes, 1991; Novak, 1999; Muñoz García and Williams, 2005), which is actually almost the same diet as *Fossa fossana*. However, these species do not have the same microwear feature, which suggests that differences observed in our microwear analysis are not due to the diet itself.

The frugivores, in spite of important standard deviations on the two variables are more clearly differentiated on the slicing facet than on the grinding one.

In the whole dataset, omnivores (*Vulpes vulpes* and *Meles meles*) are in the center of the bimodal graphs (Fig. 6) and display high standard deviation. Foxes are rather close to meat eaters, bone eaters, and insectivores. Badgers, which are more opportunists, can be divided into two sub-groups (Fig. 6). The first one displays microwear similar to that of the eater of larvae and worms and the herbivores (many scratches and few pits); the second one is closer to the frugivores, insectivores and meat eaters.

#### 4.4. Application to fossil taxa

On the representation of axes one and two for the grinding facet (Fig. 4), *Pseudocyon sansaniensis* and *Amphicyon major* are close to the group “frugivore–insectivore–meat eater–bone eater”, and as a consequence, close to *Vulpes vulpes*.

On the slicing facet (Fig. 5), the two species seem to have more distinct patterns of wear. *P. sansaniensis* has the same range of variation as the central group on the axes one, two and three and is closer to frugivores on axis three. *A. major* even if close to this group has on the first axis the same variation as malacophages, larvae and worm eaters and *Vulpes vulpes*.

On the bivariate plot (Fig. 7), Sansan amphicyonids have a medium number of scratches. *Pseudocyon sansaniensis* is near extant frugivores and *Amphicyon major* has the same range of variation as omnivores (average numbers of pits and scratches of *A. major* and of the omnivores: 187.22 and 31.78 against 218.02 and 30.70, respectively),

with a lesser standard deviation, however (Fig. 7). *A. major* has a high number of scratches nearly as much as in extant herbivores, and markedly more broad pits than in any extant taxa on the grinding facet, not illustrated here.

On all the representations the results indicate that *Pseudocyon sansaniensis* is close to the group “frugivore–insectivore–meat eater”. It suggests a diet close to frugivores but also to extant omnivores.

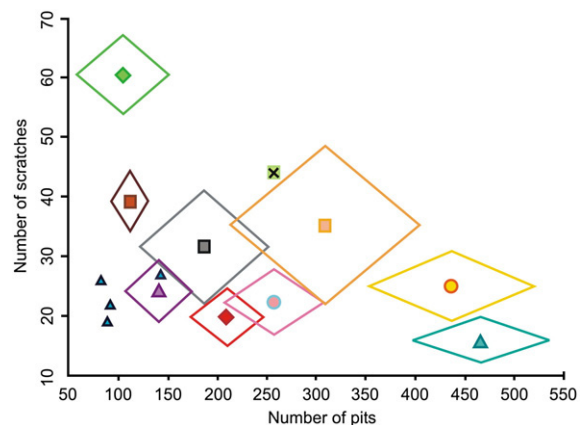
## 5. Discussion

### 5.1. Extant carnivorans

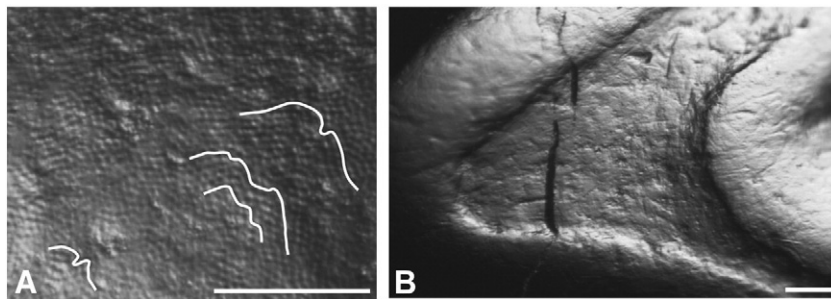
The application of the described method requires essential precautions. Cleaning and moulding the grinding facets of the smallest species of carnivorans is particularly difficult because of their limited access. This specificity has an effect on a snapshot and its analysis. Furthermore, the imperfect analogy of the lower and upper grinding facets demonstrated here on a carnivore species may constitute a barrier to the analysis of fossil taxa whose complete dentition is not always preserved. Enamel deteriorations also constitute a limit of the microwear analysis (King et al., 1999). For example, *Crocota crocuta* enamel is attacked by acid regurgitations due to its diet (Van Valkenburgh et al., 1990), which leads to an obliteration of microwear while revealing the enamel microstructure (Fig. 8A). Post-mortem alterations (Fig. 8B) can be due to fossilization and/or erosion (sandblasted surface with small pits), to the preparation and/or the excavation of the specimens (scratches of regular width, wider than 5  $\mu$ m, desiccation of the teeth). However, these alterations are easily identifiable and the concerned specimens have not been included in the final analyses.

Otherwise, species belonging to one family are not grouped together on plots or in statistical analyses. In the Ursidae, results are consistent with the diversity of diet found in this family, each species occupying a distinct pole on plots. However, the problem encountered by Evans et al. (2007) with the polar bear (the three-dimensional shape of polar bear tooth crowns, a consequence of its phylogeny, is too complex to attribute it to a carnassial feeding) does not occur here. Within Mustelidae (*Enhydra lutris*, *Lutra lutra*, and *Meles meles*) and Eupleridae (*Eupleres goudotii* and *Fossa fossana*) species also differ from one another according to their diet.

The analysis of dental microwear by optical microscopy is non-invasive and precise. In addition, we demonstrate that results do not reflect phylogenetic relationships, that microwear is highly similar on the analogous slicing facets, that the selected area on each facet is



**Fig. 7.** Number of scratches as a function of the number of pits on the slicing facet of extant (except omnivores) and extinct specimens. Diets represented by their mean and standard deviation except “Malacophage” represented by four specimens.  $\diamond$  *Leptailurus serval*,  $\diamond$  bone eater,  $\diamond$  piscivore,  $\diamond$  frugivore,  $\diamond$  herbivore,  $\diamond$  insectivore,  $\triangle$  malacophage,  $\diamond$  meat eater,  $\diamond$  larvae and worm eater,  $\diamond$  *Amphicyon major*,  $\times$  *Pseudocyon sansaniensis*.



**Fig. 8.** Examples of features and facets. A. Microstructure (underlined) on the grinding facet of *Crocota crocuta* (MNHN CG 1901-662) ( $\times 115$ ); B. Post-mortem desiccation on the grinding facet of *Mungos mungo* (MNHN CG 1962-2078) ( $\times 32$ ). Scale bar: 100  $\mu\text{m}$ .

representative of the whole facet, and that our method is reproducible at a large scale in carnivorans.

There are two main hypotheses to explain the origin of microwear features. The first is based on Baker et al. (1959), who assume that phytoliths contained in graminaceae are harder than the mammalian enamel (considered between 4.5 and 5.0 on the Moh scale [Baker et al., 1959]). Walker et al. (1978) state that the consumption of graminaceae causes the numerous scratches (Fig. 5A) observed on grazers dental facets. A lower rate of scratches is therefore seen as the consequence of a browsing diet. This is currently the most commonly accepted theory (e.g., Solounias et al., 1988; Teaford, 1991; Fortelius and Solounias, 2000; Merceron et al., 2006). Other authors proposed an alternative interpretation because results from dental microwear analyses in captive animals whose diet is known do not fit the first hypothesis (Covert and Kay, 1981). Stimulated by critics about their experimentation (see Gordon and Walker, 1983), Kay and Covert (1983) provide further support to their assumption that 1) there are no differences between chitin- and plant-fed animals, and 2) animals fed with 10% of pumice display numerous scratches. Mainland (2003, 2006) establishes that strictly grazing sheep eat more inorganic particles than mixed feeding ones and that the difference observed between seaweed-eater sheep and grazing sheep could result from differing forces or masticatory movements (Mainland, 2000). Nystrom et al. (2004) conclude that scratches observed on the teeth of *Papio hamadryas* from the Awash National Park are mainly caused by relatively small-caliber environmental grit and that small pits would be caused by enamel prisms “plucking” as suggested by Gordon (1982). Furthermore, Sanson et al. (2007) state that silica phytoliths are weaker than mammalian enamel. Therefore, the conclusion would be that at least the scratches observed on dental facets are essentially caused by terrigenous grit or dust.

Nevertheless, the hypothesis that scratches are the consequences of accidental ingestion of terrigenous or dust particles does not satisfactorily explain all of our observations on carnivorans and is questioned in Merceron et al. (2007).

Whether phytoliths have an impact on enamel is an important issue to discuss. Calcium oxalate is the most abundant insoluble mineral found in plants (Korth et al., 2006). The calcium oxalate phytoliths, less studied because they are considered less informative than silica ones in terms of taxonomy, are present in all kinds of photosynthetic organisms (Franceschi and Nataka, 2005). They constitute a defense against herbivory (Franceschi and Nataka, 2005; Korth et al., 2006). Danielson and Reinhard (1998) show that calcium oxalate phytoliths are harder than enamel (they abrade test tiles at 4.5 and 5.0 on the Moh scale) and cause numerous microwears on teeth. Even if they are weaker than enamel, calcium oxalate and silica phytoliths could have an impact in the case of herbivorous carnivorans since Richardson (1968) showed that soft abrasives can wear metals.

That said, *Eupleres goudotii* feeds on worms and larvae caught by foraging in the soil. Its prey do not have an exoskeleton, but the

analysed slicing dental facet shows a great number of scratches, which most probably results from the ingestion and chewing of soil or siliceous particles when foraging for prey. If our hypothesis is correct, the microwear of *E. goudotii* reveals its feeding habits, not its diet, and confirms the impact of terrigenous particles on teeth microwear. Results obtained in other taxa nuance the correlation between scratches and terrigenous particles, although dust or terrigenous grit cannot explain all of the microwear patterns observed in carnivorans. The most significant result is the dental microwear observed in the pandas. *Ailuropoda melanoleuca* and *Ailurus fulgens* are herbivores and feed almost exclusively on bamboo. The pandas retain a normal digestive tract; as other carnivorans, they cannot digest cellulose. As a matter of fact, given the indigestibility of bamboos, pandas must spend over half of the day feeding, which includes chewing (Wei et al., 1999, 2000; Long et al., 2004). The great panda eats every part of bamboos except the underground rhizomes, though it prefers leaves and shoots (Hu and Wei, 2004; Long et al., 2004); it may consume sand or small quantities of soil, but such behavior is extremely rare (e.g. Long et al., 2004). Parts consumed by the lesser panda almost exclusively include leaves and shoots (Wei et al., 1999). It is important to note that both species do not feed on foodstuff in contact with the ground (Chorn and Hoffman, 1978; Roberts and Gittleman, 1984). Given their behavior and ecology, the extremely great number of scratches on the slicing facet of m1 in the pandas is remarkable and cannot be explained by terrigenous grit. As other gramineous plants, bamboos are known to contain a great quantity of phytoliths (Piperno, 1988). We have no information regarding the content in the bamboo species of *Bashania* and *Fargesia* that compose the main part of the pandas diet in the wild (Wei et al., 1999; Hu and Wei, 2004), but previous studies showed that leaves and roots of e.g., *Phyllostachys* spp., are especially rich in silica phytoliths (e.g., Lux et al., 2003; Li et al., 2006). These bamboos are even classified among the silicon accumulating plants. Therefore, in the case of pandas, phytoliths are likely to be the main cause of the observed microwear. Another questioned result is the presence of scratches on the slicing facet of the sea otter (*Enhydra lutris*) and the polar bear (*Ursus maritimus*). Even though they are less numerous than in *Eupleres goudotii* they cannot be explained by terrigenous grit or dust since those species feed in environments located far from potential sources. Inversely, the European river otter (*Lutra lutra*) often eats its prey on land (Kruuk, 2006) but has a low amount of scratches (25 on average) and a great amount of small pits (366.75 on average). The attrition in the last case must have an impact because fish flesh is not really erosive by itself. The serval (*Leptailurus serval*) also has few scratches (16 on average) and numerous small pits (372.5 on average). It appears that manducation has a significant role in the microwear type produced. Van Valkenburgh et al. (1990) have distinguished carnivoran microwears based on the proportion of consumed bones. The cheetah (*Acinonyx jubatus*) is remarkable in avoiding the most capacious bones when it catches prey and consumes them. *L. serval* swallows (without mastication) its small prey and avoids large mammal bones. That may



be why it is differentiable from the other meat eaters of our database. Here again the attrition has an impact on observed microwear features. However, the masticatory movements in carnivores is laterally limited (Janis, 1995), and thus attrition would have more or less the same impact on all the species studied here. The other micro-features observed would, consequently, be due to abrasion.

Broad features observed on the slicing facet of malacophages and bone eaters could be related to the consumption of hard and resistant items. Bone eaters crush bones before ingesting them and malacophages break mollusc shells and crustacean exoskeletons to reach soft parts. Consuming hard items results in a low number of pits and scratches. Most importantly, the proportion of broad scratches and broad pits compared to the total number of scratches and pits respectively is greater in bone eaters and malacophages than in other taxa (30% N bP vs. 23% and 27% N bS vs. 18%). This assertion confirms Teaford's (1988) results on primates (hard feeders show numerous pits generally larger than leaf eaters ones). Consuming large hard items would then result in few but large microwear features on the slicing facet.

Frugivores are the only species having a moderate number of pits and scratches. They also display great standard deviations for these variables. Kay (1987) shows that hard and soft fruit consumers can be differentiated thanks to their microwear features. Then, the results obtained here may be the consequence of kinkajou mixed diet: this animal eats insects, fruits containing a core (hard object causing few broad features) but also less tough items such as berries and fruit with seeds that result in more but narrower microwear features (Ford and Hoffman, 1988).

Meat eaters display few scratches and a moderate number of pits. Their proportion of broad scratches is relatively large and could be the consequence of contacts with bones. Insectivores, close to meat eaters on plots, have a larger number of pits that may result from the consumption of insect cuticles, which are both rigid and plastic (Vincent and Wegst, 2004).

The disparate diet of omnivores causes a median type of microwear, having a great standard deviation. But they have different microwear types. The lack of available information on badger specimens does not allow us to relate the observation of two sub-groups to a sexual dimorphism or ontogenetic, seasonal, or geographical variations.

Microwear analysis in extant carnivores enables the determination of food preferences and the proportions of hard items consumed. On the slicing facet, the number of pits, scratches, broad pits, fine pits, broad scratches and fine scratches are sufficient to distinguish each diet represented in our database. It is noticeable that no extant species produce a microwear pattern with both numerous pits and numerous scratches. Does this result correspond to an unexploited ecological niche, to a maximum level of wear on facets or to an artifact result due to our limited database?

On the grinding facet, these basic variables are less representative than on the slicing one. However, the number of gaps (N G) is informative on the grinding facet. It is strongly related to the number of broad pits, a variable more characteristic of the grinding phase of chewing. Ovoid pits, absent on the slicing facets, are present in some species only. Ovoid pits are representative of a wear due to consumption of small hard objects, in particular seeds as from berries in extant ungulates (Solounias and Semprebon, 2002; Merceron et al., 2005b). They are observable on some specimens of *Potos flavus* (Fig. 3A). Curved scratches (little scratches forming an arc) are observed in Hyaenidae, in particular *Hyaena hyaena* (Fig. 3B) on this facet.

## 5.2. Fossil carnivores

With seven individuals, *Amphicyon major* comprises enough individuals to assume its diet. The slicing facet suggests an omnivore diet with a remarkable meat-eater tendency. Actually, based on previous studies, *A. major* was not expected to eat fruits, insects and larvae. The present study, however, reveals some affinities with the red fox, an extant canid known to have such a diet. This is surprising given the difference of size

between the two species. *Pseudocyon sansaniensis* shows significantly different results, and has a reconstructed diet closer to that of the European badger, with more plant parts than in *A. major*. Results from the grinding facet of *A. major* indicate a diet clearly distinct from that of all extant species included here. A great number of scratches and, above all, many broad pits, suggests a diet comprising a significant proportion of plants and hard items. These results therefore confirm the duality of the carnassial of *Amphicyon* and *Pseudocyon*. However, they contrast with previous statements like Ginsburg's (1999) since, at least in *A. major* from Sansan, the slicing facet reveals more similarities with the fox than with the felids, and the grinding facet indicates a significant portion of vegetation (high number of scratches) and hard items, presumably bones (high number of broad pits). The number of broad pits on the grinding facet of *A. major* is much greater than in *Crocota crocuta* (Fig. 4), which is probably due to the different location of the crushing function in these animals, in P3/p3 in the spotted hyena and in the posterior molars in amphicyonids. This is confirmed by the relative high number of broad pits in malacophages, which have their crushing function posteriorly located, as in *A. major*. It is important to notice that, while extant species discriminate better on the slicing facet, *P. sansaniensis* and *A. major* are also distinguishable from other species on the grinding one (bivariate plot and axis 3 of the PCA). Moreover, although information given by the grinding facet is less discriminating, it is more or less similar on the slicing facet for extant species. This is not the case for the studied fossil species. Is it due to the duality of their molars and/or the importance of their grinding surface or was *A. major* occupying an ecological niche unused by extant carnivores?

Viranta (1996) proposed that *Pseudocyon sansaniensis* was less adapted for bone crushing than *Amphicyon* spp. Our analysis on the grinding facet indicates that in Sansan, the diet of this species included the same amount of hard items than that of *Amphicyon major* (Fig. 4), but this is based on a single individual of *P. sansaniensis*.

## 6. Conclusions

Based on a completely new and original database, this study shows that microwear analysis by optical stereomicroscopy can be applied to most carnivores. Results are reproducible, statistically significant and permit us to distinguish the various diets tested. Microwear is not related to phylogeny, and mechanical, physical, or chemical deteriorations can be easily identified. However, a large number of specimens must initially be tested in order to determine precisely the bias affecting in comparisons between extant and extinct species.

Dental microwear analysis on fossil material results in more precise information and allows us to correct previous assumptions made on the diet of two Amphicyonidae based only on the dental or cranial morphology. Thus, dental microwear analysis does not confirm previous hypotheses that *Amphicyon* spp. are primarily carnivorous (e.g., Sorkin, 2006), omnivores (e.g., Hunt, 2003) or bone-crushing mesocarnivore (e.g., Viranta, 1996). According to the present study, *Amphicyon major* and *Pseudocyon sansaniensis* are not primarily carnivorous. Their diet includes a large portion of hard items and plants. Both species are omnivores, fox-like for *A. major*, badger-like for *P. sansaniensis*. However, in comparison with the omnivore extant taxa included here (*Vulpes vulpes*, *Meles meles*), these amphicyonids ate a greater proportion of hard items (presumably bones) and plant material, and *A. major* more so than *P. sansaniensis*.

The numbers of scratches, pits, broad scratches, broad pits, fine scratches and fine pits are sufficiently discriminant to distinguish diets on the slicing facet. Curved scratches and ovoid pits may also be representative of well defined diets on the grinding facet. It would be interesting to test if other variables like length and orientation of scratches provide additional information as in Charles et al. (2007).

As a consequence of our discussion, we acknowledge that numerous parameters may have an impact on microwear formation. Among them, consumed items but also grit or dust presence in the environment, silica and/or calcium oxalate phytoliths presence and

hardness in the food, attrition phenomenon, mandible shape (phylogenetically and/or pathologically determined), duration and strength of mastication, and manducation habits should be further studied. For example, microwear analysis could be coupled with a morpho-functional study among carnivorans (of teeth, masticatory muscles and dependent osseous structures) and with a behavioral study in order to better understand the relation between manducation, masticatory scheme and microwear formation.

It would also be interesting to quantify the bias implied by the appearance of microstructure on occlusal surfaces and the impact of enamel microstructure on the wear and the microwear of Carnivora to complete the work of Maas (1991). Even if the causes of different microwear features observed are not totally explained, it not only enables us to differentiate diets (especially on the slicing facet) but also to make assumptions on the relative proportions of large hard items consumed. Thus, carnivorans eating a great proportion of flesh have a microwear different from those consuming more bone. Also needed is, a systematic study of dental microwears of common species like foxes and badgers from the same area, but that were killed or died during different seasons, to assess the effect of the seasonality on the proportion of each microwear feature. Lastly, microwear analysis can be even more objective thanks to the use of 3-D scanners and with the total automation of data processing (Scott et al., 2005, 2006; Merceron et al., 2006). These possible applications and improvements would permit us to better understand the formation of microwear and could allow a better comprehension of fossil ecosystems.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2008.09.004.

## References

Anyonge, W., 1996. Microwear on canines and killing behavior in large carnivores: saber function in *Smilodon fatalis*. *Journal of Mammalogy* 77, 1059–1067.

Anyonge, W., Baker, A., 2006. Craniofacial morphology and feeding behaviour in *Canis dirus*, the extinct Pleistocene dire wolf. *Journal of Zoology* 269, 309–316.

Baker, G., Jones, L.H.P., Wardrop, I.D., 1959. Cause of wear in sheep's teeth. *Nature* 184, 1583–1584.

Balter, V., Person, A., Labourdette, N., Drucker, D., Renard, M., Vandermeersch, B., 2001. Les Néandertaliens étaient-ils essentiellement carnivores? Résultats préliminaires sur les teneurs en Sr et en Ba de la paléobiocénose mammalienne de Saint-Césaire. *Comptes-rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des planètes* 332, 59–65.

Biknevicius, A.R., 1996. Functional discrimination of the masticatory apparatus in cougar (*Puma concolor*) and spotted hyena (*Crocuta crocuta*) juveniles and adults. *Canadian Journal of Zoology* 74, 1934–1942.

Biknevicius, A.R., Ruff, C.B., 1992. Structure of the mandibular corpus and its relationship to feeding behaviours in extant carnivorans. *Journal of Zoology* 228, 478–507.

Biknevicius, A.R., Van Valkenburgh, B., Walker, J., 1996. Incisor size and shape: Implications for feeding behaviors in saber-toothed "cats". *Journal of Vertebrate Paleontology* 16 (3), 510–521.

Binder, W.J., Van Valkenburgh, B.V., 2000. Development of bite strength and feeding behaviour in juvenile spotted hyenas (*Crocuta Crocuta*). *Journal of Zoology* 252, 273–283.

Bocherens, H., Drucker, D., 2003. Trophic level isotopic enrichment and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems. *International Journal of Osteoarchaeology* 13, 46–53.

Boesi, R., Biancardi, C.M., 2002. Diet of the Eurasian badger *Meles meles* (Linnaeus 1758) in the natural reserve of Lago di Piano, Northern Italy. *Mammalian Biology* 67, 120–125.

Butler, P.M., 1946. The evolution of carnassial dentitions in the Mammalia. *Proceedings of the Zoological Society of London* 116, 198–220.

Charles, C., Jaeger, J.-J., Michaux, J., Viriot, L., 2007. Dental microwear in relation to changes in the direction of mastication during the evolution of Myodonta (Rodentia, Mammalia). *Naturwissenschaften* 94, 71–75.

Chorn, J., Hoffman, R.S., 1978. *Ailuropoda melanoleuca*. *Mammalian species* 110, 1–6.

Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., De Ruiter, D., 2005. Animal diets in the Waterberg based on stable isotopic composition of faeces. *South African Journal of Wildlife Research* 35, 45–52.

Covert, H.H., Kay, R.F., 1981. Dental microwear and diet: implications for determining the feeding behaviors of extinct primates, with a comment on the dietary pattern of *Sivapithecus*. *American Journal of Physical Anthropology* 55, 331–336.

Danielson, D.R., Reinhard, K.J., 1998. Human dental microwear caused by calcium oxalate phytoliths in prehistoric diet of the lower Pecos region, Texas. *American Journal of Physical Anthropology* 107, 297–304.

De Master, D.P., Stirling, I., 1981. *Ursus maritimus*. *Mammalian species* 145, 1–7.

De Muizon, C., Lange-Badré, B., 1997. Carnivorous dental adaptations in tribosphenic mammals and phylogenetic reconstruction. *Lethaia* 30, 353–366.

Dewar, E.W., 2003a. Functional diversity within the Littleton fauna (early Paleocene), Colorado: evidence from body mass, tooth structure, and tooth wear. *Paleobios* 23 (1), 1–19.

Dewar, E.W., 2003b. Microwear of carnivorous mammals described by low-magnification dental stereomicroscopy. *Journal of Vertebrate Paleontology* 24, 52 A.

Emerson, S.B., Radinsky, L., 1980. Functional-analysis of sabertooth cranial morphology. *Paleobiology* 6 (3), 295–312.

Estes, J.A., 1980. *Enhydra lutris*. *Mammalian species* 133, 1–8.

Estes, R.D., 1991. *Behavior Guide to African Mammals*. University of California Press, Berkeley.

Evans, A.J., Wilson, G.P., Fortelius, M., Jernvall, J., 2007. High-level dentition in carnivorans and rodents. *Nature* 445, 78–81.

Feranec, R.S., 2004. Isotopic evidence of saber-tooth development, growth rate, and diet from the adult canine of *Smilodon fatalis* from Rancho La Brea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206, 303–310.

Flynn, J.J., Finarelli, J.A., Zehr, S., Hsu, J., Nedbal, M.A., 2005. Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology* 54, 317–337.

Ford, L.S., Hoffman, R.S., 1988. *Potos flavus*. *Mammalian species* 321, 1–9.

Fortelius, M., Soloumias, N., 2000. Functional characterization of ungulate molars using the abrasion–attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* 3301, 1–36.

Franceschi, V.R., Nataka, P.A., 2005. Calcium oxalate in plants: formation and function. *Annual Review of Plant Biology* 56, 41–71.

Garbutt, N., 1999. *Mammals of Madagascar*. Yale University Press, New Haven.

Ginsburg, L., 1961. La faune des carnivores miocènes de Sansan (Gers). *Mémoires du Muséum national d'Histoire naturelle Série C, Sciences de la Terre* 9, 1–190.

Ginsburg, L., 1999. Order Carnivora. In: Rössner, G.E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, Munich, pp. 109–148.

Ginsburg, L., Bulot, C., 2000. La faune miocène de Sansan et son environnement: Le cadre stratigraphique du site de Sansan. *Mémoires du Muséum national d'Histoire naturelle* 183, 1–392.

Gordon, K.D., 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. *American Journal of Physical Anthropology* 59, 195–215.

Gordon, K.D., Walker, A.C., 1983. Playing 'possum': a microwear experiment. *American Journal of Physical Anthropology* 60, 109–112.

Gorniak, G.C., Gans, C., 1980. Quantitative assay of electromyograms during mastication in domestic cats (*Felis catus*). *Journal of morphology* 163, 253–281.

Grine, F.E., 1987. Quantitative analysis of occlusal microwear in *Australopithecus* and *Paranthropus*. *Scanning Microscopy* 2, 647–656.

Hainard, R., 1989. Mammifères sauvages d'Europe. Insectivores – Chéiroptères – Carnivores. Delachaux and Niestlé, Neuchâtel, Switzerland.

Herfst, M.S., 1984. Habitat and food of the otter *Lutra lutra* in Shetland. *Lutra* 27, 57–70.

Hiemae, K.M., 1978. Mammalian mastication: a review of the activity of the jaw muscles and the movements they produce in chewing. In: Butler, P.M., Joysey, K.A. (Eds.), *Development, Function and Evolution of teeth*. Academic Press, New York, pp. 359–398.

Holliday, J.A., Steppan, S.J., 2004. Evolution of hypercarnivory: the effect of specialisation on morphological and taxonomic diversity. *Paleobiology* 30 (1), 108–128.

Hu, J., Wei, F., 2004. Comparative ecology of giant pandas in the five mountain ranges of their distribution in China. In: Lindburg, D., Baragona, K. (Eds.), *Giant Pandas – Biology and Conservation*. University of California Press, Berkeley, pp. 137–148.

Hunt Jr., R.M., 1998. Amphicyonidae. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.), *Evolution of Tertiary Mammals of North America. Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals, vol. 1*. Cambridge University Press, London, pp. 196–227.

Hunt Jr., R.M., 2003. Intercontinental migration of large mammalian Carnivores: earliest occurrence of the Old World bearded *Amphicyon* (Carnivora, Amphicyonidae) in North America. *Bulletin of the American Museum of Natural History* 279, 77–115.

Janis, C.M., 1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. In: Boucot, A.J. (Ed.), *Evolutionary Paleobiology of Behavior and Coevolution*. Elsevier, Amsterdam, pp. 241–259.

Janis, C.M., 1995. Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. In: Thomason, J.J. (Ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge, pp. 76–98.

- Kay, R.F., 1987. Analysis of dental microwear using image processing techniques. *Scanning Microscopy* 1, 657–662.
- Kay, R.F., Covert, H.H., 1983. True grit: a microwear experiment. *American Journal of Physical Anthropology* 61, 33–38.
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *American Journal of Physical Anthropology* 108, 359–373.
- Korth, K.L., Doege, S.J., Park, S.-H., Goggin, F.L., Wang, Q., Gomez, S.K., Liu, G., Jia, L., Nakata, P.A., 2006. *Medicago truncatula* mutants demonstrate the role of plant calcium oxalate crystals as an effective defense against chewing insects. *Plant Physiology* 141, 188–195.
- Kruuk, H., 2006. *Otters Ecology, Behaviour and Conservation*. Oxford University Press, Oxford.
- Lanszki, J., 2004. Diet of badgers living in a deciduous forest in Hungary. *Mammalian Biology* 69, 354–358.
- Legendre, S., Roth, C., 1988. Correlation of carnassial tooth size and body weight in recent carnivores (Mammalia). *Historical Biology* 1, 85–98.
- Lartet, E., 1836. Nomenclature des mammifères et des coquilles qu'il a trouvés dans un terrain d'eau douce près de Simorre et de Sansan (Gers). *Bulletin de la Société géologique de France* 7, 217–220.
- Li, Z., Lin, P., He, J., Yang, Z., Li, Y., 2006. Silicon's organic pool and biological cycle in moso bamboo community of Wuyishan Biosphere Reserve. *Journal of Zhejiang University, Science B* 7, 849–857.
- Long, Y., Lu, Z., Wung, D., Zhu, X., Wang, H., Zhang, Y., Pan, W., 2004. Nutritional strategy of giant pandas in the Qinling Mountains of China. In: Lindburg, D., Baragona, K. (Eds.), *Giant Pandas — Biology and Conservation*. University of California Press, Berkeley, pp. 90–100.
- Lux, A., Luxova, M., Abe, J., Morita, S., Inanaga, S., 2003. Silicification of bamboo (*Phyllostachys heterocycla* Mitf.) root and leaf. *Plant and Soil* 255, 85–91.
- Maas, M.C., 1991. Enamel structure and microwear: an experimental study of the response of enamel to shearing force. *American Journal of Physical Anthropology* 85, 31–49.
- Mainland, I.L., 2000. A dental microwear study of seaweed-eating and grazing sheep from Orkney. *International Journal of Osteoarchaeology* 10, 93–107.
- Mainland, I.L., 2003. Dental microwear in grazing and browsing Gotland sheep (*Ovis aries*) and its implications for dietary reconstruction. *Journal of Archaeological Science* 30, 1513–1527.
- Mainland, I.L., 2006. Pastures lost? A dental microwear study of ovicaprine diet and management in Norse Greenland. *Journal of Archaeological Science* 33, 238–252.
- McKenna, M.C., Bell, S.K., 1997. *Classification of Mammals Above the Species Level*. Columbia University Press, New York.
- Meiri, S., Dayan, T., Simberloff, D., 2005. Variability and correlations in carnivore crania and dentition. *Functional Ecology* 19, 337–343.
- Merceron, G., Madelaine, S., 2006. Molar microwear pattern and palaeoecology of ungulates from La Berbie (Dordogne, France): environment of Neanderthals and modern human populations of the Middle/Upper Palaeolithic. *Boreas* 35, 272–278.
- Merceron, G., Ungar, P., 2005. Dental microwear and palaeoecology of bovids from the Early Pliocene of Langebaanweg, Western Cape province, South Africa. *South African Journal of Science* 101, 365–370.
- Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., Heintz, E., 2004. The Late Miocene paleoenvironment of Afghanistan as inferred from dental microwear in artiodactyls. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207, 143–163.
- Merceron, G., Blondel, C., De Bonis, L., Koufos, G.D., Viriot, L., 2005a. A new method of dental microwear analysis: application to extant primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). *Palaio* 20, 551–561.
- Merceron, G., De Bonis, L., Viriot, L., Blondel, C., 2005b. Dental microwear of fossil bovids from northern Greece: paleoenvironmental conditions in the eastern Mediterranean during the Messinian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 217, 173–185.
- Merceron, G., De Bonis, L., Viriot, L., Blondel, C., 2005c. Dental microwear of the late Miocene bovids of northern Greece: Vallesian/Turolian environmental changes and disappearance of *Ouranopithecus macedoniensis*? *Bulletin de la Société Géologique de France* 176, 475–484.
- Merceron, G., Taylor, S., Scott, R., Chaimanee, Y., Jaeger, J.-J., 2006. Dietary characterization of the hominoid *Khoratpithecus* (Miocene of Thailand): evidence from dental topographic and microwear texture analysis. *Naturwissenschaften* 93, 329–333.
- Merceron, G., Schultz, E., Kordos, L., Kaiser, T.M., 2007. Paleoenvironment of *Dryopithecus brancoi* at Rudabánya, Hungary: evidence from dental meso- and microwear analyses of large vegetarian mammals. *Journal of Human Evolution* 53 (4), 331–349.
- Muñoz García, A., Williams, J.B., 2005. Basal metabolic rate in carnivores is associated with diet after controlling for phylogeny. *Physiological and Biochemical Zoology* 78, 1039–1056.
- Novak, R.M., 1999. *Walker's Mammals of the World*. The Johns Hopkins University Press, Baltimore.
- Nystrom, P., Phillips-Conroy, J.E., Jolly, C.J., 2004. Dental microwear in Anubis and hybrid baboons (*Papio hamadryas*, *sensu lato*) living in Awash National Park, Ethiopia. *American Journal of Physical Anthropology* 125, 279–291.
- Piperno, D.R., 1988. *Phytoliths Analysis. An Archaeological and Geological Perspective*. Academic Press, London.
- Popowicz, T.E., 2003. Postcanine dental form in the Mustelidae and Viverridae (Carnivora, Mammalia). *Journal of Morphology* 256, 322–341.
- Rensberger, J.M., 1978. Scanning Electron Microscopy of wear and occlusal events in some small herbivores. In: Butler, P.M., Joysey, K.A. (Eds.), *Development, Function, and Evolution of Teeth*. Academic Press, New York, pp. 415–438.
- Rensberger, J.M., 1997. Enamel microstructural specialization in the canine of the spotted hyena, *Crocuta crocuta*. *Scanning Microscopy* 13, 343–361.
- Richardson, R.C.D., 1968. The wear of metals by relatively soft abrasives. *Wear* 11 (4), 245–275.
- Rieger, L., 1981. *Hyaena hyaena*. *Mammalian species* 150, 1–5.
- Roberts, M.S., Gittleman, J.L., 1984. *Ailurus fulgens*. *Mammalian species* 222, 1–8.
- Roth, J.D., Hobson, K.A., 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. *Canadian Journal of Zoology* 78, 848–852.
- Sacco, T., Van Valkenburgh, B., 2004. Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). *Journal of Zoology* 263, 41–54.
- Schaller, G.B., Qitao, T., Johnson, K.G., Xiaoming, W., Heming, S., Jinchu, H., 1989. The feeding ecology of giant pandas and asiatic black bears in the Tangjiahe reserve, China. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology, and Evolution*, vol. 1. Cornell University Press, Ithaca, pp. 212–241.
- Sanson, G.D., Kerr, S.A., Gross, K.A., 2007. Do silica phytoliths really wear mammalian teeth? *Journal of Archaeological Science* 34, 526–531.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436, 693–695.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, M.F., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. *Journal of Human Evolution* 51 (4), 339–349.
- Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? *Journal of Human Evolution* 47, 115–144.
- Sillen, A., Lee-Thorp, J.A., 1994. Trace element and isotopic aspects of predator–prey relationships in terrestrial foodwebs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 243–255.
- Solounias, N., Hayek, L.A.C., 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. *Journal of Zoology* 229, 421–445.
- Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulates ecomorphology with application to early fossil equids. *American Museum Novitates* 3366, 1–49.
- Solounias, N., Teaford, M., Walker, A., 1988. Interpreting the diet of extinct ruminants: the case of a non browsing giraffid. *Paleobiology* 14, 287–300.
- Sorkin, B., 2006. Ecomorphology of the giant bear-dogs *Amphicyon* and *Ischyrocyon*. *Historical Biology* 18, 375–388.
- Sponheimer, M., Robinson, T., Ayliffe, L., Passey, B., Roeder, B., Shipley, L., Lopez, E., Cerling, T., Dearing, D., Ehleringer, J., 2003. An experimental study of carbon-isotope fractionation between diet, hair, and faeces of mammalian herbivores. *Canadian Journal of Zoology* 81, 871–876.
- Taylor, M.E., Hannam, A.G., 1986. Tooth microwear and diet in the African Viverridae. *Canadian Journal of Zoology* 65, 1696–1702.
- Teaford, M.F., 1988. A review of dental microwear and diet in modern mammals. *Scanning Microscopy* 1, 1149–1166.
- Teaford, M.F., 1991. Dental microwear: what can it tell us about diet and dental function? In: Larsen, M.A., Kelley, C.S. (Eds.), *Advances in Dental Anthropology*. Alan R. Liss, New York, pp. 341–356.
- Teaford, M.F., Oyen, O.J., 1989. *In vivo* and *in vitro* turnover in dental microwear. *American Journal of Physical Anthropology* 80, 447–460.
- Teaford, M.F., Walker, A., 1984. Dental microwear and diet in two species of *Colobus*. In: Else, J.G., Lee, P.C. (Eds.), *Primate Ecology and Conservation*. Cambridge University Press, Cambridge, pp. 63–66.
- Therrien, F., 2005. Feeding behaviour and bite force of sabretoothed predators. *Zoological Journal of the Linnean Society* 145, 393–426.
- Tüzün, I., Albayrak, I., 2005. The effect of disturbances to habitat quality on otter (*Lutra lutra*) activity in the river Kızılırmak (Turkey): a case study. *Turkish Journal of Zoology* 29, 327–335.
- Van Valkenburgh, B., 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology* 14 (2), 155–173.
- Van Valkenburgh, B., 1989. Carnivore dental adaptation and diet: a study of trophic diversity within guilds. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology, and Evolution*. Cornell University Press, Ithaca, pp. 410–435.
- Van Valkenburgh, B., 1994. Extinction and replacement among predatory mammals in the North American Late Eocene and Oligocene: tracking a paleoguild over twelve million years. *Historical Biology* 8, 1–22.
- Van Valkenburgh, B., Ruff, C.B., 1987. Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology* 212, 379–397.
- Van Valkenburgh, B., Teaford, M.F., Walker, A., 1990. Molar microwear and diet in the sabretooth cat, *Smilodon fatalis*. *Journal of Zoology* 222, 319–340.
- Vincent, J.F.V., Wegst, U.G.K., 2004. Design and mechanical properties of insect cuticle. *Arthropod Structure & Development* 33, 187–199.
- Viranta, S., 1996. European Miocene Amphicyonidae — taxonomy, systematics and ecology. *Acta Zoologica Fennica* 204, 1–61.
- Virgós, E., Mangas, J.G., Blanco-Aguilar, J.A., Garrota, G., Almagro, N., Viso, R.P., 2004. Food habits of European badgers (*Meles meles*) along an altitudinal gradient of Mediterranean environments: a field test of the earthworm specialization hypothesis. *Canadian Journal of Zoology* 82, 41–51.
- Walker, A., Hoeck, H.N., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. *Science* 201, 908–910.
- Wei, F., Feng, Z., Wang, Z., Zhou, A., Hu, J., 1999. Use of nutrients in bamboo by the red panda (*Ailurus fulgens*). *Journal of Zoology* 248, 535–541.
- Wei, F., Wang, Z., Feng, Z., Li, M., Zhou, A., 2000. Seasonal energy utilization in bamboo by the red panda (*Ailurus fulgens*). *Zoo Biology* 19, 27–33.